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Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees

Abstract Seasonal regulation of leaf water potential (Ψ_L) was studied in eight dominant woody savanna species growing in Brazilian savanna (Cerrado) sites that experience a 5-month dry season. Despite marked seasonal variation in precipitation and air saturation deficit (D), seasonal differences in midday minimum Ψ_L were small in all of the study species. Water use and water status were regulated by a combination of plant physiological and architectural traits. Despite a nearly 3-fold increase in mean D between the wet and dry season, a sharp decline in stomatal conductance with increasing D constrained seasonal variation in minimum Ψ_L by limiting transpiration per unit leaf area (E). The leaf surface area per unit of sapwood area (LA/SA), a plant architectural index of potential constraints on water supply in relation to transpirational demand, was about 1.5–8 times greater in the wet season compared to the dry season for most of the species. The changes in LA/SA from the wet to the dry season resulted from a reduction in total leaf surface area per plant, which maintained or increased total leaf-specific hydraulic conductance (G_t) during the dry season. The isohydric behavior of Cerrado tree species with respect to minimum Ψ_L throughout the year thus was the result of strong stomatal control of evaporative losses, a decrease in total leaf surface area per tree during the dry season, an increase in total leaf-specific hydraulic conductance, and a tight coordination between gas and liquid phase conductance. In contrast with the seasonal isohydric behavior of minimum Ψ_L, predawn Ψ_L in all species was substantially lower during the dry season compared to the wet season. During the dry season, predawn Ψ_L was more negative than bulk soil Ψ estimated by extrapolating plots of E versus Ψ_L to $E = 0$. Predawn disequilibrium between plant and soil Ψ was attributable largely to nocturnal transpiration, which ranged from 15 to 22% of the daily total. High nocturnal water loss may also have prevented internal water storage compartments from being completely refilled at night before the onset of transpiration early in the day.

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Introduction

Isohydric plants can maintain nearly constant leaf water potentials (Ψ_L) throughout the year despite changes in soil and atmospheric conditions (Tardieu and Simonneau 1998). Some of the mechanisms that allow this homeostatic behavior have been outlined by Whitehead (1998). For example, when the air saturation deficit increases, a concomitant decrease in stomatal conductance or total leaf surface area can limit transpiration, thereby constraining variation in minimum Ψ_L. On the other hand, if the leaf-specific conductance of the soil/leaf pathway increases, stomatal conductance should increase, as long as the air saturation deficit and total leaf surface area remain constant (Whitehead 1998). This coordination between the gas phase and liquid phase conductance has been observed in several species (e.g., Meinzer and Grantz 1990; Lloyd

et al. 1991; Meinzer et al. 1999; Comstock 2000). In many Neotropical savanna woody species, minimum Ψ_L remains nearly constant throughout the year, despite the occurrence of a prolonged dry season (Medina and Francisco 1994; Franco 1998). The mechanisms contributing to this homeostatic behavior in savanna trees have not been fully studied.

The savannas of central Brazil, characterized by a 3- to 5-month dry season, oligotrophic soils, and frequent fires, are the second most extensive plant formation in South America after the lowland tropical rain forests (Eiten 1972). The Brazilian savannas are composed of grasses with relatively shallow roots and deeply rooted evergreen and deciduous woody plants. The term Cerrado is commonly used in two ways: (1) to describe the broad Cerrado phytogeographic region with an area of 2.0×10^6 km^2, and (2) to describe one of the three primary structural types of plant communities that make up the Cerrado region. The consequences of seasonal drought for physiological activity of woody Cerrado species have been studied for only a limited number of species and the results appear to be contradictory. Ferri (1944) concluded that many Cerrado woody species transpired freely throughout the year, whereas only a few species restricted their transpiration during the dry season. The explanation offered to account for this putative weak stomatal control of transpiration in some Cerrado tree species is continuous access to deep soil water (Goodland and Ferri 1979). Indeed, many Cerrado woody species have root systems at least 10 m deep (Sarmiento 1983). At the stand level, however, Miranda et al. (1997) reported substantial reduction in both leaf area index and evapotranspiration during the dry season in a Cerrado site. However, the micrometeorological techniques used by these authors did not distinguish between the relative contributions of herbaceous and woody plants to total water loss. More recently, Meinzer et al. (1999), using heat dissipation probes to measure sap flow, observed strong stomatal limitation of transpiration before midday in four evergreen species during the dry season.

Nocturnal transpiration may prevent the plant water potential from reaching equilibrium with that of the soil (Donovan et al. 1999, 2001; Bucci et al. 2004) and may also prevent internal water storage compartments from being refilled before the onset of transpiration early in the day. Nocturnal transpiration and its consequences have been studied in relatively few species because it is generally assumed that stomata are uniformly closed at night or that nighttime vapor pressure near the leaf surface is at or near saturation. However, some recent reports indicate that, under certain environmental conditions, nocturnal water loss can be relatively high (Benyon 1999; Donovan et al. 1999; Oren et al. 1999a; Bucci et al. 2004). In one extreme case, the contribution of nocturnal water loss to total daily water loss was about 50% (Feild and Holbrook 2000). In Cerrado sites, relative humidity can be very low during the dry season. Values of about 10% relative humidity during the day and 40–50% at night are frequently observed. Thus, with the relatively high nocturnal temperatures typical of tropical savanna sites and the low relative humidity, the vapor pressure difference between leaf and air could re-

sult in appreciable nocturnal transpiration rates if stomata are not completely closed (Bucci et al. 2004). All of this may have consequences for the water economy of Cerrado woody plants by enhancing leaf water deficits and by preventing internal homeostatic mechanisms from operating adequately.

The main objectives of the present study were to characterize seasonal variation in plant water balance, and to explore the mechanisms underlying the observed seasonal patterns of midday and predawn Ψ_L in eight dominant woody species growing in Cerrado sites in central Brazil. Sap flow, Ψ_L, soil-to-leaf hydraulic conductance, leaf area to sapwood area ratios, the contribution of nocturnal transpiration to daily water loss, and environmental variables were measured at the peak of the wet and dry seasons. It was hypothesized that the isohydric behavior of Cerrado tree species with respect to minimum midday Ψ_L throughout the year is the result of strong stomatal control of transpiration, a decrease in total leaf surface area per tree during the dry season, and a tight coordination between gas and liquid phase conductance. It was also hypothesized that the significant differences in predawn Ψ_L between the wet and dry seasons can be partially explained by substantial nocturnal transpiration during the dry season.

Materials and methods

Study site and plant material

The study was carried out at the Instituto Brasileiro de Geografia e Estatistica (IBGE) ecological reserve, a field experimental station located 33 km south of the center of Brasilia, Brazil (latitude 15°56′, longitude 47°53′ W, altitude 1,100 m). The IBGE includes extensive areas of all major physiognomic forms of Cerrado vegetation from very open to closed savannas. The study area was located in savannas with intermediate tree density. Annual precipitation in the reserve ranges from 880 to 2,150 mm with a mean of approximately 1,500 mm. There is a pronounced dry season from May through September with the months of June, July, and August being nearly rainless. Mean annual temperature is about 22°C, with small seasonal changes. Maximum diurnal air temperature differences, on the other hand, can be as large as 20°C during a typical dry season day. The soils are very deep oxisols with a high percentage of clay. Despite their high clay content, the soils behave like coarser-textured soils and are extremely well-drained.

Field measurements were made toward the end of the dry season during the months of August and September of 1999 and 2000 and at the peak of the wet season during the months of January and February of 1999 and 2000. Eight dominant woody species ranging from evergreen to brevideciduous and deciduous were selected for the study: *Schefflera macrocarpa* (C & S.) Seem (Araliaceae) evergreen, *Styrax ferrugineus* Ness et Mart., (Styracaceae) evergreen, *Blepharocalyx salicifolius* (H.B. & K.) Berg. (Myrtaceae) evergreen, *Ouratea hexasperma* (St. Hil.) Baill (Ochnaceae) evergreen, *Caryocar brasiliense* Camb.,

(Caryocaraceae) brevideciduous, *Erythroxylum suberosum* St. Hil (Erythroxylaceae) brevideciduous, *Qualea parviflora* Mart., (Vochyseaceae) deciduous, and *Kielmeyera coriaceae* (Spr) Mart. (Guttiferae) deciduous. All the species renew leaves during the dry season with the exception of *S. macrocarpa*, which produces new leaves continuously throughout the year. The brevideciduous species are functionally evergreen because they seldom remain leafless for more than a few days. However, most evergreen species also show progressive leaf senescence and abscission during the dry season. *K. coriaceae* remains leafless for about a month depending on the severity of the dry season. Height of the species studied ranged from 5.3 ± 0.9 m in *S. ferrugineus* to 1.8 ± 0.03 m in *E. suberosum,* and stem external diameter ranged from 11.0 ± 0.4 cm in *S. ferrugineus* to 5.9 ± 0.4 cm in *K. coriaceae*.

Sap flow and water potentials

Whole-plant sap flow was measured during 2–3 consecutive days in each of three to five individuals per species during dry and wet seasons. The heat dissipation method described by Granier (1985, 1987) was used. Briefly, a pair of 20-mm long, 2-mm diameter probes (UP, Munich, Germany) was inserted into the sapwood near the base of the main stem in each plant. The upper (downstream) probe contained a copper-constantan thermocouple and a heating element of constantan, which was continuously heated at a constant power by the Joule effect, while the unheated upstream probe served as a temperature reference. Temperature differences between the upstream and downstream probes were recorded every 10 s, and 10 min averages were stored in solid-state storage modules (SM192, Campbell Scientific, Logan, Utah) connected to dataloggers (CR 10X, Campbell Scientific). The sapwood depth in the stems of the individuals studied ranged from 3 to 6 cm, and consequently the 20-mm probes used spanned most of the hydroactive portion of the xylem.

Sap flux density was calculated from the temperature difference between the two probes using an empirical calibration (Granier 1985, 1987) recently re-validated for tropical trees (Clearwater et al. 1999). Mass flow of sap per individual was obtained by multiplying flux density by sapwood cross-sectional area. The relationship between sapwood cross-sectional area and stem diameter was obtained by injecting dye near the base of the main stem for several individuals of each species representing a range of diameters. After 2 h the plants were decapitated a few cm above the point of dye injection and the area of conducting tissue was determined from the pattern of staining by the dye as it moved in the transpiration stream. Transpiration per unit leaf area was obtained by dividing the mass flow of sap by the total leaf area per plant. Total leaf area per plant was obtained by multiplying the number of leaves per plant by the average area per leaf determined from a subsample of 10–50 leaves per plant.

Leaf water potential (Ψ_L) was measured with a pressure chamber (PMS, Corvallis, Ore.). Typically, six to seven sets of measurements were obtained during the course of a day for each species during the dry and wet seasons (three different leaves from each of three to five individuals).

Stomatal and hydraulic conductance, and environmental variables

A steady-state porometer (Model LI-1600, LiCor, Lincoln, Neb.) was used to measure stomatal conductance (g_s) on three most recently fully expanded leaves of the same plants used for sap flow measurements. Typically, six to seven complete sets of measurements were obtained during the course of a day during both seasons.

The apparent leaf area-specific hydraulic conductance of the soil/root/leaf pathway (G_t) was determined as

$$G_t = E/\Delta\Psi_L$$

where $\Delta\Psi_L$ is the difference between the current Ψ_L and the Ψ of the bulk soil, and *E* is the average transpiration rate per unit leaf area determined from sap flow measurements at the time Ψ_L was determined. During the dry season, when predawn Ψ_L was not expected to reflect that of the bulk soil due to substantial nocturnal transpiration, bulk soil Ψ was estimated by extrapolating the Ψ_L–*E* relationships obtained by simultaneous measurements of Ψ_L and *E* throughout the day to *E*=0 (Sperry et al. 2002). A morphological index of potential transpirational demand relative to water transport capacity was obtained for each individual fitted with sap flow sensors by dividing the total leaf area by the sapwood area near the base of the main stem (LA/SA).

Air temperature and relative humidity were monitored with humidity probes (HMP35C, Vaisala, Helsinki, Finland) at an automated weather station installed at the site. Data were recorded continuously with a datalogger and solid state storage module similar to those used for the sap flow measurements. Air saturation deficit (*D*) was calculated from relative humidity and air temperature.

Results

Annual precipitation in the study area was 1,206 and 1,706 mm for 1999 and 2000, respectively. Precipitation was restricted mostly to the months of September through April (Fig. 1). Mean *D* varied seasonally from a minimum of about 0.5 kPa in the wet season to a maximum of about 1.5 kPa during the dry season. Despite marked seasonal variation in precipitation and *D*, and consequently in water potential in the upper portion of the soil profile, no significant differences in midday Ψ_L between the wet and dry seasons were observed in any of the study species (Fig. 2a). In *C. brasiliense*, midday Ψ_L was 0.12 MPa more negative in the wet season than in the dry season. In the remaining seven species, midday Ψ_L was 0.08–0.46 MPa more negative during the dry season, but the species-specific differences were not statistically significant. On the other hand, predawn Ψ_L was significantly lower
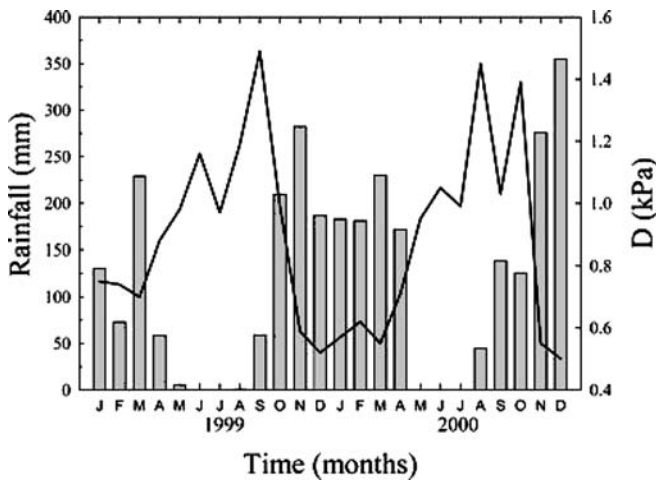
Fig. 1 Seasonal variations in mean monthly precipitation and air saturation deficit (*D*) from January 1999 to December 2000 at the Instituto Brasileiro de Geografia e Estatistica (IBGE) research station. *Bars* Precipitation, *solid line D*
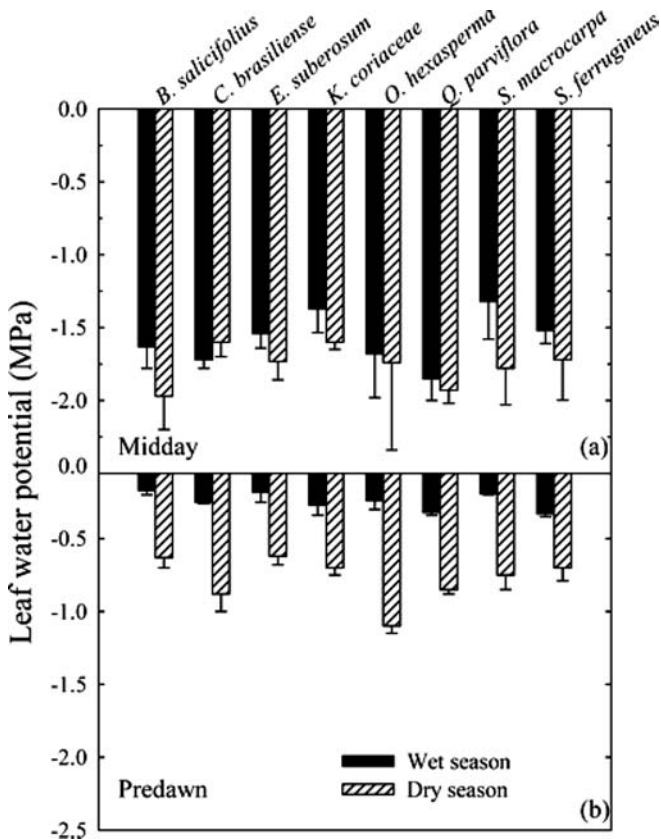

Fig. 2 Midday (**a**) and predawn (**b**) leaf water potentials during the wet and dry seasons of 1999 and 2000 for eight Cerrado woody species. *Bars* Means ± SE (*n* = three to five trees per species)

($P < 0.05$, Mann Whitney non-parametric test) during the dry season compared to the wet season, across all species (Fig. 2b).

Total leaf area per plant varied seasonally (data not shown). Consequently, average LA/SA, a tree architectural index of potential constraints on water supply in relation to transpirational demand, was about 1.5–8 times higher

in the wet season compared to the dry season, except for *B. salicifolius*, in which LA/SA increased, but not significantly ($P > 0.1$), during the dry period (Table 1). Most of the seasonal changes in LA/SA were the result of a large decrease in leaf surface area during the dry season because sapwood area (the active portion of the xylem) did not substantially change from wet to dry seasons. Consistent with the similarity in midday Ψ_L among seasons, total daily sap flow did not differ significantly between wet and dry seasons for six of the eight study species. On the other hand, total daily transpiration per unit leaf area (*E*) was significantly higher during the dry season (Table 1), with the exception of *S. macrocarpa*.

Stomatal conductance (g_s) declined with increasing *D* in a similar fashion across all species, allowing stomatal response to *D* to be described with a single function that accounted for 80% of the variation in g_s (Fig. 3). Mean maximum G_t ($G_{t\,max}$) decreased exponentially with increasing LA/SA across species, with $G_{t\,max}$ tending to be higher for most species during the dry season (Fig. 4). A single function adequately described the relationship between $G_{t\,max}$ and LA/SA for all eight species during both seasons with LA/SA accounting for >70% of the variation in $G_{t\,max}$. Leaf water potential decreased linearly with increasing *E* in all eight species during both the wet and dry seasons (Fig. 5). The Ψ_L–*E* relationships were extrapolated to $E = 0$ in order to obtain an estimate of the bulk soil Ψ (Sperry et al. 2002) independent of predawn Ψ_L (Fig. 5). These estimated values of soil Ψ were consistently higher (more positive) than the values of predawn Ψ_L observed during the dry season (Fig. 2b). The estimated values of bulk soil Ψ during the wet season, also obtained from the extrapolation of the Ψ_L–*E* relationships to $E = 0$, were not significantly different from zero ($P > 0.1$, one sample *t*-test), consistent with the high (close to zero) predawn leaf water potentials measured during the wet season.

Stomatal conductance was positively correlated with G_t (Fig. 6). During the wet season all species conformed to the same linear relationship between g_s and G_t. However, during the dry season a unique linear relationship fitted to each species better described the dependence of g_s on G_t. Maximum values of G_t tended to be higher during the dry season than during the wet season, and the slopes of the linear relationships tended to be lower compared to the single linear relationship fitted to all wet season data.

Seasonal variation in g_s (expressed as the ratio of g_s in dry season to that in the wet season) was negatively correlated with the ratio of LA/SA during the dry season to that during the wet season (Fig. 7), signifying that species with larger decreases in LA/SA from the wet to the dry season tended to exhibit smaller declines in g_s during the dry season. In *K. coriaceae*, for example, similar g_s during the dry and wet seasons was associated with an 8-fold decrease in LA/SA during the dry season, whereas the absence of significant seasonal adjustment in LA/SA in *B. salicifolius* was associated with a sharp decline in g_s during the dry season.

Predawn Ψ_L declined with increasing nighttime water loss expressed as a percentage of the daily total

Table 1 Average leaf area:sapwood area (LA/SA) ratio, daily sap flow per plant and daily transpiration per unit leaf surface area, in individuals (n = three to five) of the eight study species in both the wet and dry seasons. Values are means ($\pm$1SE) of 2–3 days of sap flow. Values followed by different letters are significantly different ($P<0.05$)

| Species	LA/SA ($m^2\ cm^{-2}$)		Daily sap flow ($kg\ day^{-1}$)		Daily transpiration ($mol\ m^{-2}\ day^{-1}$)	
	Wet	Dry	Wet	Dry	Wet	Dry
Blepharocalyx salicifolius	0.148±0.039	0.207±0.052	8.3±2.9 a	3.8±1.0 b	136±60 a	29±7 b
Caryocar brasiliense	0.09±0.030 a	0.017±0.007 b	4.3±1.2	6.1±1.7	104±32 a	494±42 b
Erythroxylum suberosum	0.073±0.013 a	0.03±0.007 b	1.2± 0.2	1.0±0.0	107±14 a	229±35 b
Kielmeyera coriaceae	0.057±0.012 a	0.007±0.004 b	1.7±0.4 a	0.2±0.1 b	150±11 a	357±100 b
Ouratea hexasperma	0.130±0.043	0.059±0.027	2.8± 1.4	2.0±0.6	57±6 a	103±20 b
Qualea parviflora	0.145±0.006 a	0.073±0.038 b	2.2±1.4	1.3±0.6	34±5 a	200±44 b
Schefflera macrocarpa	0.134±0.047	0.095±0.020	3.9±1.7	1.5±1.0	95±12	76±29
Styrax ferrugineus	0.063±0.013 a	0.014±0.002 b	5.9±1.2	4.3±1.3	125±21 a	349±143 b
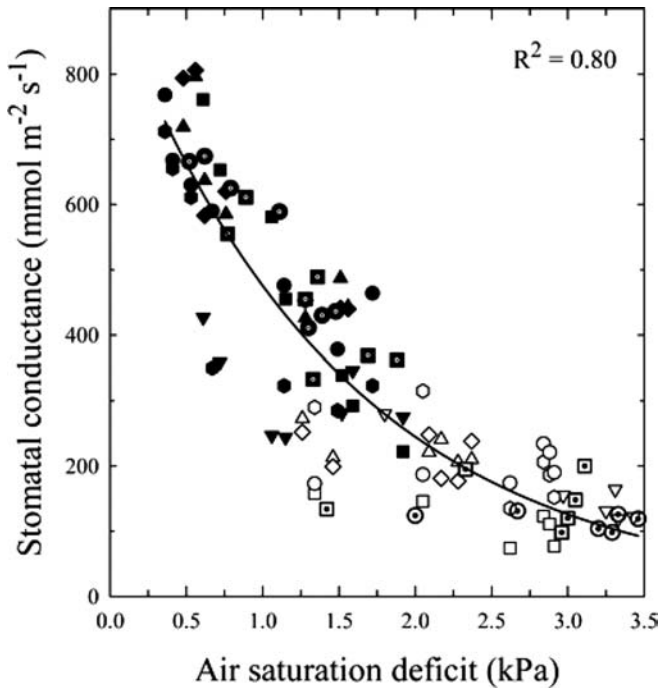
Fig. 3 Relationship between stomatal conductance and air saturation deficit (D) for eight Cerrado woody species during the wet (*solid symbols*) and dry (*open symbols*) seasons. Each point represents the average stomatal conductance for three to five individuals per species at different times during the day from 0900 to 1800 hours, under nonlimiting light conditions. *Solid line* Negative exponential function fitted to the data. △ ▲ *Schefflera macrocarpa*, ○ ● *Styrax ferrugineus*, ▽ ▼ *Ouratea hexasperma*, *Blepharocalyx salicifolius*, ◇ ◆ *Erythroxylum suberosum*, open circle, solid hexagon *Caryocar brasiliense*, open square with black dot, solid square with white dot *Qualea parviflora*, □ ■ *Kielmeyera coriaceae*

Fig. 4 Relationship between the maximum apparent leaf area-specific hydraulic conductance of the soil/root/leaf pathway ($G_{t\ max}$) and the leaf area/sapwood area ratio (LA/SA) for individuals of eight Cerrado woody species. Each point represents the value for a single individual. *Open symbols* Values obtained during the dry season, *solid symbols* values obtained during the wet season, *solid line* negative exponential function fitted to the data. *Symbols as in Fig. 3*

transpiration (Fig. 8a). Nocturnal transpiration ranged from 3 to 15% during the wet season and from 15 to 22% of the daily total during the dry season. The difference between predicted soil water potential determined by extrapolating the Ψ_L vs. sap flow relationship for each species to zero flow in Fig. 5 and predawn Ψ_L of freely transpiring plants (Ψ_{soil} − predawn Ψ_L) was also correlated with nocturnal water use (Fig. 8b). The Ψ_{soil} − predawn Ψ_L values, which can be considered an estimate of the soil to leaf water potential disequilibrium, became more positive (larger disequilibrium) with increasing nocturnal water use.
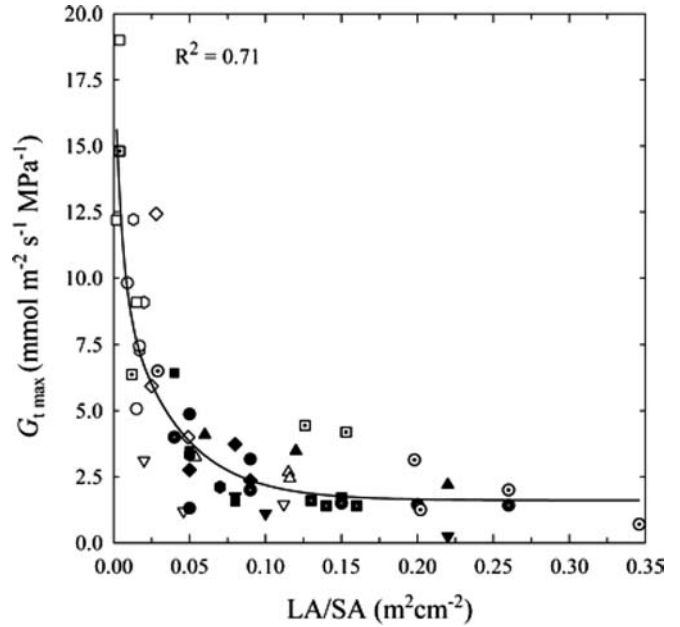
Discussion

Homeostasis of midday leaf water potentials

Minimum Ψ_L of all eight tree species studied was similar during the dry and wet seasons. Our results were consistent with previous reports of an absence of pronounced seasonal differences in water status of Cerrado woody plants (e.g., Franco 1998; Meinzer et al. 1999). Seasonal changes in leaf water status are determined in part by soil water availability. Despite a 4- to 5-month dry season, the presence of permanently moist soil at depths below 2 m in many Cerrado sites (Rawitscher 1948) indicates that much of the annual precipitation of 1,500 mm remains unexploited by the tree roots that explore deeper soil layers than herbaceous
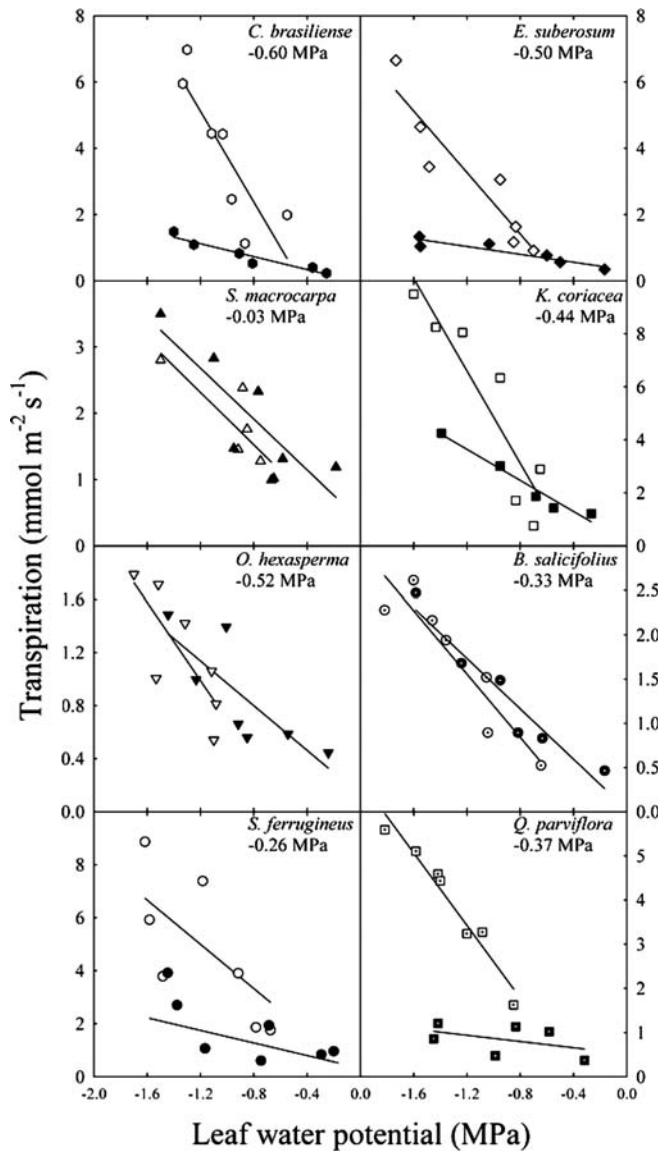
Fig. 5 Relationship between transpiration rate and leaf water potential (Ψ_L) for eight Cerrado woody species during wet and dry seasons. *Open symbols* Values obtained during the dry season, *solid symbols* values obtained during the wet season. Each point represents the average transpiration rate and Ψ_L for three to five individuals per species at different times during the day. *Solid lines* Linear regressions fitted to data. The *x*-intercept values (predicted Ψ_L at zero transpiration) for the dry season data are included in each panel. *Symbols* as in Fig. 3

Fig. 6 Relationship between stomatal conductance (g_s) and apparent leaf area-specific hydraulic conductance of the soil/root/leaf pathway (G_t). Each point represents average of g_s, and G_t for three to five individuals per species measured during the course of 1 day during the wet (*closed symbols*) and dry (*open symbols*) seasons. *Solid lines* Linear regressions fitted to data. A different linear regression for each species was fitted for the dry season data (*open symbols*): *Schefflera macrocarpa* R^2: 0.68, *Styrax ferrugineus* R^2=0.84, *B. salicifolius* R^2=0.50, *E. suberosum* R^2=0.68, *C. brasiliense* R^2=0.96. In the remaining three species, the linear regressions for the dry season data were not statistically significant ($P>0.1$). *Symbols* as in Fig. 3

Fig. 7 Ratio of stomatal conductance (g_s) between dry and wet seasons as a function of the LA/SA ratio between dry and wet seasons. The ratios represent the fractional decrease in g_s and the fractional increase in LA/SA for each species during the dry season. Each point represents values for a single individual. *Solid line* Negative exponential function fitted to the data. *Symbols* as in Fig. 3

vegetation. However, even though roots of many Cerrado woody species can tap abundant soil water, substantially higher D during the dry season could be expected to result in more negative minimum water potentials than during the wet season. Why then is dry season minimum Ψ_L not significantly different from that measured during the wet season? Our results suggest that both physiological and allometric responses contributed to seasonal homeostasis of minimum Ψ_L.

The impact of increased atmospheric evaporative demand on transpiration during the dry season was limited by the negative correlation between g_s and D (Fig. 3). The
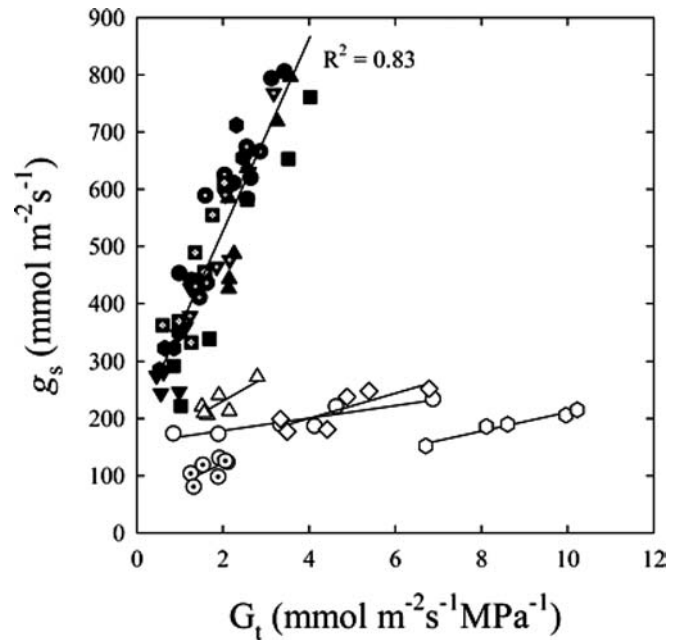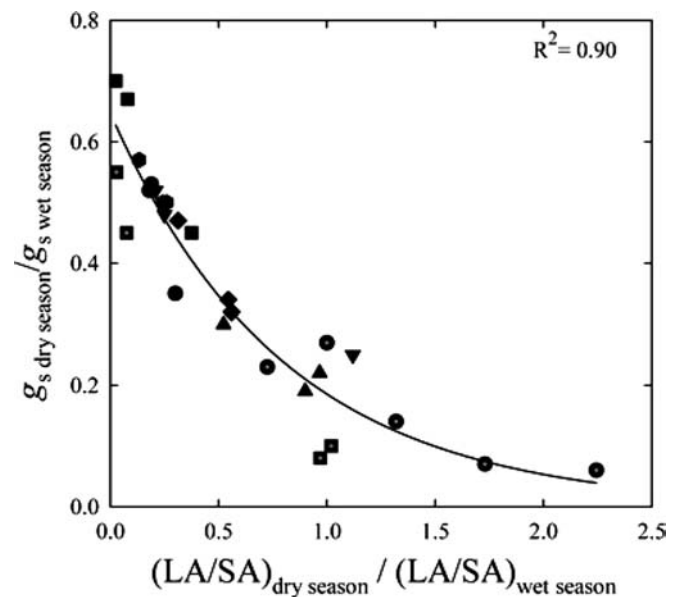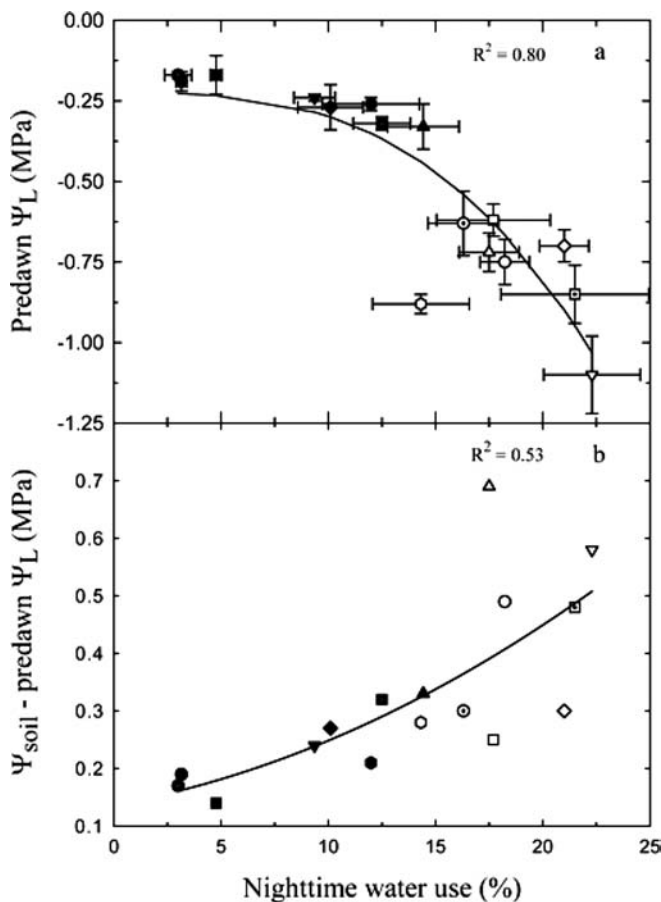
Fig. 8 Relationship between (**a**) predawn Ψ_L and nighttime water use (percent of daily total water loss) and (**b**) $\Psi_{soil} -$ predawn Ψ_L (an estimate of the soil to leaf water potential disequilibrium) and nighttime water use. Each point represents the average value (± 1SE) of three to five individuals per species. *Open symbols* Values obtained during the dry season, *solid symbols* values obtained during the wet season. *Symbols* as in Fig. 3

relatively high coefficient of determination (R^2=0.80) obtained when a single function was used to describe the dependence of g_s on D for all eight species was consistent with suggestions that intrinsic stomatal responsiveness to humidity is similar in diverse species when covariation in other plant and environmental variables influencing g_s is taken into account (Meinzer et al. 1995, 1997). When the data in Fig. 3 were analyzed according to the procedure proposed by Oren et al. (1999b), the sensitivity of g_s to increasing D (dg_s/dln$D$) for a reference value of g_s=475 mmol m^{-2} s^{-1} at D=1 kPa was consistent with a hydraulic model that assumes stomatal regulation of Ψ_L above a critical minimum value. Nevertheless, the observed reductions in g_s at high D were not sufficient to prevent E from increasing substantially during the dry season in six of the eight species studied (Table 1). Therefore, it is likely that additional mechanisms contributed to seasonal homeostasis of minimum Ψ_L. For example, reductions in Ψ_L associated with increased E can be offset by compensatory increases in G_t (Whitehead 1998). In the present study, G_t tended to be greater during the dry season (Figs. 4 and 6), suggest-

ing that, in addition to stomatal response to D, seasonal adjustments in G_t contributed to homeostasis of minimum Ψ_L. Although several factors can contribute to variation in G_t, seasonal variation in LA/SA associated with shedding of leaves appeared to be the major component of seasonal variation in G_t (Fig. 4). At the whole-plant level, similar or reduced total daily sap flow during the dry season despite a 3-fold increase in D, was a consequence of both reduced leaf area per plant and stomatal responses to humidity.

Despite the overall similarity in the dependence of $G_{t\,max}$ on LA/SA among all eight species studied, and higher values of $G_{t\,max}$ during the dry season across most species, there were discernible differences among species in their operating ranges of G_t (Fig. 4). For example, *Q. parviflora* tended to operate over a broad range from 1.6 to 14.8 mmol m^{-2} s^{-1} MPa^{-1}, whereas *O. hexasperma* tended to operate at values of G_t below 4.5 mmol m^{-2} s^{-1} MPa^{-1}. There was no relationship between leaf phenology and the operating ranges of G_t and E. Although a common linear relationship between g_s and G_t was observed across all eight species during the wet season, during the dry season several unique linear relationships were observed (Fig. 6). Why was convergence in the relationship between g_s and G_t observed only during the wet season? During the dry season, leaves were in different stages of development, from expanding to senescent. Stomatal conductance measurements were made on the most recently expanded leaves, but these leaves were not necessarily in the same developmental stage, and therefore might not have provided a consistent estimate of actual vapor flux during the dry season. Differences in stomatal responses to D in different type of leaves, as well as relatively large changes in stem capacitance, may have caused the relationships between g_s and G_t to vary. Furthermore, the proportion of leaves in different phenological stages differed among species, which may explain why, despite the lack of convergence in the relationship between g_s and G_t during the dry season, the relationship between E and G_t was adequately described by a single function during both the dry and wet seasons (results not shown). The linear relationships between g_s and G_t suggest that transpiration was limited by stomatal adjustment to variation in G_t over the entire range of G_t observed (Meinzer et al. 1999).

Nocturnal transpiration and predawn disequilibrium between plant and soil water potential

Our results indicate that, during the dry season when nighttime D remains relatively high, nocturnal transpiration by Cerrado woody species can be considerable. In seven of the eight species studied, between 15% and 25% of the total daily water loss occurred at night (Fig. 8). These percentages are within the range of nighttime/daytime water loss observed for other species from different ecosystems (e.g., Benyon 1999; Donovan et al. 2001). The heat dissipation method for estimating sap flow requires that the lowest temperature difference between the two thermocouple probes, usually attained at night, be set to zero for flow calculations (Granier 1985, 1987). This

procedure should underestimate total nocturnal water loss. We have validated the heat dissipation method using heat pulse techniques for estimating sap flow (Scholz et al. 2002) and both methods produced similar overall nocturnal sap flows (results not shown). Calculations based on stomatal conductance measurements also indicated that nocturnal water loss is a relatively large fraction of the total daily water loss in Cerrado woody plants (Bucci et al. 2004). It has been shown that nocturnal transpiration can prevent overnight equilibration between plant and soil Ψ, with important implications for the widespread use of predawn Ψ_L as a surrogate for the volume-averaged Ψ of the soil in which the plant is rooted (Donovan et al. 1999, 2001, 2003; Bucci et al. 2004). However, even when plant and soil Ψ do not equilibrate overnight, a good estimate of the bulk soil Ψ can be obtained by extrapolating the trajectory of a plot of E versus Ψ_L to $E=0$ provided soil Ψ remains relatively constant when E increases (Sperry et al. 2002).

In the present study, predawn Ψ_L was universally more negative during the dry season than during the wet season (Fig. 2). When plots of E versus Ψ_L during the dry season were extrapolated to $E=0$, the estimated values of bulk soil Ψ were substantially more positive than measured predawn Ψ_L (cf. Figs. 2 and 5). Our results therefore suggest that the differences between the estimated bulk soil Ψ and the measured predawn Ψ_L reflected plant-soil Ψ disequilibrium associated with nocturnal transpiration. Even during the wet season, nocturnal transpiration may have been sufficient to prevent overnight equilibration of plant and soil Ψ in several of the study species (Fig. 8). The potential adaptive significance, if any, of nocturnal transpiration in Cerrado woody species is not clear, but it is possible that having stomata partly open during the early morning when incident light is increasing rapidly and D is still relatively low, may enhance water-use efficiency and permit additional morning carbon gain before g_s is restricted by high D in the afternoon. Regardless of the role of nocturnal stomatal opening in the carbon economy of Cerrado woody plants, nocturnal transpiration will prevent equilibration between leaf and soil Ψ at night, which may have important consequences for plant water economy, particularly with regard to operation of internal homeostatic mechanisms for maintaining Ψ_L above threshold minimum values.

Conclusions

Seasonal patterns of water use and water status of Cerrado woody species appear to be regulated by a combination of plant architectural and physiological traits. Although roots of some Cerrado species can penetrate to depths of 10 m or more, hydraulic constraints and substantially higher evaporative demand during the dry season could result in larger leaf water deficits unless compensatory mechanisms operate to limit water loss or enhance the relative efficiency of water supply on a leaf area basis. The isohydric behavior of Cerrado tree species with respect to minimum Ψ_L throughout the year was the result of strong stomatal control of evaporative losses, a decrease in total leaf surface area per tree during the dry season, an increase in total leaf-specific hydraulic conductance, and a tight coordination between gas and liquid phase conductance. In contrast with the isohydric behavior of minimum Ψ_L between wet and dry season, predawn Ψ_L in all species was substantially lower during the dry season compared to the wet season. During the dry season, predawn Ψ_L was more negative than bulk soil Ψ estimated by extrapolating plots of E versus Ψ_L to $E=0$. Predawn disequilibrium between plant and soil Ψ was attributable largely to nocturnal transpiration, which ranged from 15 to 22% of the daily total.

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